

Additions to the Genus *Phyllodesmium*, with a Phylogenetic Analysis and its Implications to the Evolution of Symbiosis

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Abstract. The facelinid genus *Phyllodesmium* (Ehrenberg, 1831) consists of approximately 24 described species that prey upon soft-bodied corals. At least five additional species have yet to be described, making it an interesting genus for testing phylogenetic hypotheses. The genus is extremely morphologically diverse, with many species adapting specifically to a specific host coral. One of the most interesting adaptations found in this genus is the widespread participation in a symbiotic relationship with photosynthetic dinoflagellates in the genus *Symbiodinium*. Two new species, *Phyllodesmium acanthorhinum* n. sp. and *Phyllodesmium undulatum* n. sp., from the Philippine Islands and Japan are described, and a morphological phylogeny is created to include the two new species, as well as three undescribed species. An examination of the *Phyllodesmium* phylogeny suggests that species with digestive gland branching and zooxanthellae are more derived. Confidence and robustness in this analysis are lacking, however, and further studies using molecular data could add confidence to this conclusion.

INTRODUCTION

The facelinid genus *Phyllodesmium* (Ehrenberg, 1831) consists of approximately 24 described species that prey upon soft-bodied corals. At least five species have yet to be described, making it an interesting genus for taxonomic and phylogenetic studies (Burghardt and Gosliner, 2006; Burghardt et al., 2008a; Moored Gosliner, 2009). While this paper was in press, eight additional species were described (Burghardt et al., 2008a). Each newly described species leads to exciting discoveries about the adaptive history of this group, and adds another piece to the evolutionary puzzle. One of the most interesting adaptations found in this genus is the widespread participation in a symbiotic relationship with photosynthetic dinoflagellates (zooxanthellae) in the genus *Symbiodinium*. Many species of *Phyllodesmium* are able to retain zooxanthellae, which they obtain from their aleyonarian food source (Kempf, 1984; Rudman, 1981, 1991). This is a unique relationship compared to other *Symbiodinium* symbioses because the nudibranchs are not the primary host of the zooxanthellae (Rudman, 1981). Instead, the nudibranch consumes and digests the coral, the primary host of the symbiont, while selectively preserving and translocating intact zooxanthellae into the cells of the digestive gland.

Symbiotic *Phyllodesmium* species have branched digestive glands that often ramify into the cerata and dorsal surface of the body, where exposure to sunlight is at its highest. Once harvested, the zooxanthellae are passed into these branches and the nudibranch receives nutrients produced by the photosynthesizing algae.

Histological studies have shown a positive correlation between the extent of digestive gland branching and the zooxanthellae retention abilities of these nudibranchs. Highly specialized species are able to accumulate vast amounts of zooxanthellae in extensively branched digestive tissue, maximizing the photosynthetic product they receive from their stolen symbionts. Based on this observation, Rudman (1991) suggested that animals with minimal or no branching, and thus few or no zooxanthellae, are more primitive species, whereas animals with vastly branched digestive tissue have further evolved to accommodate algal symbionts. Although correlative evidence supports this idea, phylogenetic study to support this hypothesis has not been completed, and long-term starvation experiments have just recently begun (Burghardt et al., 2005, 2008b; Burghardt & Gosliner, 2006; Burghardt & Wägele, 2006). In addition, phylogenies based on genetic characters (Moored Gosliner, 2011) and have been published.

Another interesting aspect of the symbiotic relationship in the genus *Phyllodesmium* is the variation in ability to retain zooxanthellae. Some species, such as *Phyllodesmium opalescens* Rudman, 1991, are completely aposymbiotic and digest the algae with the rest of their prey, or sometimes pass the cells unharmed. Some, such as *Phyllodesmium hyalinum* Ehrenberg, 1831, can retain the algae for a short time, and others, like *Phyllodesmium longicirrum* (Bergh, 1905), and *Phyllodesmium briareum* (Bergh, 1896) have extremely advanced mutualistic relationships that allow them to survive significant periods of time in the absence of a food source (Rudman, 1981, 1991; Kempf, 1991; Burghardt et al.,

Table 1

Literature references used to create the data matrix for phylogenetic analysis.

Taxon	Reference
<i>Favorinus japonicus</i>	Baba, 1949; Rudman, 1980
<i>Godiva quadricolor</i>	Willan, 1987
<i>P. horridum</i>	Rudman, 1981, 1991
<i>P. serratum</i>	Rudman, 1991; Baba, 1991a
<i>P. opalescens</i>	Rudman 1991
<i>P. poindimiei</i>	Rudman, 1981, 1991
<i>P. briareum</i>	Rudman, 1991; Gosliner et al., 1996
<i>P. colemani</i>	Rudman, 1991
<i>P. magnum</i>	Rudman 1991
<i>P. parangatum</i>	Ortiz & Gosliner, 2003
<i>P. hyalinum</i>	Rudman, 1981, 1991; Baba, 1991b
<i>P. crypticum</i>	Rudman, 1981, 1991
<i>P. macphersonae</i>	Rudman, 1981, 1991; Baba 1991b
<i>P. longicirrum</i>	Rudman, 1981, 1991
<i>P. guamensis</i>	Avila et al., 1998
<i>P. pecten</i>	Rudman, 1981
<i>P. iriomotense</i>	Baba, 1991b. This study
<i>P. kabiramanu</i>	Baba, 1991b
<i>P. jakobsenae</i>	Burghardt & Wägele, 2004
<i>P. rudmani</i>	Burghardt & Gosliner, 2006
<i>P. acanthorhinum</i> n. sp.	This study
<i>P. undulatum</i> n. sp.	This study
<i>P. tuberculatum</i>	Moore & Gosliner, 2009
<i>P. pinnatum</i>	Moore & Gosliner, 2009
<i>P. karenae</i>	Moore & Gosliner, 2009

2005, 2008b). *Phyllodesmium longicirrum* is especially notable, housing thriving communities of algae. This species may even cultivate populations of zooxanthellae by regularly digesting a fraction of the symbionts (Rudman, 1981; Kempf, 1991). The range of intimacy between the nudibranch and zooxanthellae that exists within species of *Phyllodesmium* makes it an ideal place to study the progression of symbiosis as it evolved in these animals (Wägele, 2004).

In this study, two new species of *Phyllodesmium* are described using anatomical dissections and scanning electron micrographs. An updated phylogeny that includes the new species was then generated based on morphological characters.

METHODS

Drawings of anatomical structures were completed using a Nikon SMZ-U binocular microscope with drawing tube. Buccal mass structures were coated with gold/palladium using a Denton Desk II vacuum sputter coater, and scanning electron micrographs were produced by a LEO 1450 VP scanning electron microscope. Specimens were deposited at the California Academy of Sciences in the Invertebrate Zoology Department collection (CASIZ).

Using anatomical characters, a morphological phylogeny was created to infer placement of the new species

and to map symbiosis within the genus. Using the character matrix constructed by Ortiz & Gosliner (2008) as a guide, characters and character states were reevaluated by careful examination of the literature (Table 1). When necessary and possible, dissection of specimens was used to decipher character states that were not made clear by descriptions in the literature. The reevaluated characters were then entered into MacClade 4 software (Maddison & Maddison, 2005) to generate an updated matrix (Table 2). As was done by Ortiz & Gosliner (2008), *Godiva quadricolor* (Barnhard, 1927) and *Favorinus japonicus* Baba, 1949, were retained as outgroups due to their likely relationship with species of *Phyllodesmium*. Other characters and character states, however, were modified from the previous study. Parsimony analysis was conducted using a heuristic search with 100 replicates of starting trees using random stepwise additions in PAUP 4.0 (Swofford 2002). All uninformative characters were excluded from the analysis, as well as character number 2. This character was difficult to quantify and was removed to avoid confounding the data set. A permutation tail probability test was conducted using PAUP to determine if the resulting phylogenetic tree is significantly different from randomness. Decay analysis was performed using a heuristic search in PAUP for all trees greater than or equal to the shortest trees obtained.

RESULTS

Phyllodesmium acanthorhinum n. sp.

(Figures 1A; 2A; 4A, B; 5A, B; 8A)

Phyllodesmium spec. Wägele et. al, 2006: 38, figure 5I.

Phyllodesmium spec. 6 Gosliner et. al, 2008: 389, bottom photo.

Material examined

Holotype: California Academy of Sciences, CASIZ 099093, 3–4 m depth, near Onna Village, Horseshoe Cliffs, Okinawa, Ryukyu Islands, Japan, 1 July 1994, R. F. Bolland.

Paratypes: Three specimens, two dissected, CASIZ 104702, 3–4 m depth, near Onna Village, Horseshoe Cliffs, Okinawa, Ryukyu Islands, Japan, 8 July 1994, R. F. Bolland.

Geographic range

This species is known from the Horseshoe Cliffs, Okinawa, Ryukyu Islands, Japan (this study) and

Table 2

Character states present in species of *Phyllodesmium* and outgroups *G. quadricolor* and *F. japonicus*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	
<i>Favorinus japonicus</i>	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	?	1	?	0	?	?	0	1	1	1	0	
<i>Godiva quadricolor</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	
<i>P. horridum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	0	0	1	0	1	1	0	2
<i>P. serratum</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	?	?	?	1		
<i>P. opalescens</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1
<i>P. poindiriei</i>	1	0	1	0	0	1	1	0	0	0	1	1	1	1	0	1	1	2	?	0	0	0	0	0	0	0	1	0	1	1	1	3	
<i>P. briareum</i>	0	1	2	1	0	0	0	0	0	0	1	1	1	1	0	0	1	2	?	0	0	1	1	1	0	0	0	0	1	1	1	2	
<i>P. colemani</i>	0	1	2	1	0	1	0	0	0	0	1	1	1	1	0	1	1	2	?	1	1	1	1	1	0	0	0	0	1	1	0	4	
<i>P. magnum</i>	1	0	2	1	0	1	1	0	0	0	1	1	1	1	0	0	1	2	?	1	1	1	1	0	0	0	1	0	1	0	1	3	
<i>P. parangatum</i>	1	0	2	1	0	1	1	1	0	0	1	1	1	1	0	0	1	1	1	0	1	0	0	1	0	1	1	0	1	0	1	1	
<i>P. hyalinum</i>	0	0	2	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0	1	0	1	0	0	1	1	1	3	
<i>P. crypticum</i>	1	0	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	?	0	0	1	1	3	
<i>P. macphersonae</i>	0	1	2	1	0	1	1	0	0	0	1	1	1	1	0	1	1	2	?	0	0	0	0	0	0	?	0	0	0	1	1	1	
<i>P. longicirrum</i>	1	0	2	1	0	1	1	0	0	0	1	1	1	0	0	0	1	2	?	1	1	1	1	1	0	?	1	0	1	0	1	3	
<i>P. guamensis</i>	1	0	2	1	0	1	1	1	0	0	1	1	1	1	0	0	1	2	?	0	1	0	1	1	1	0	0	0	1	1	0	3	
<i>P. pecten</i>	0	0	2	?	0	1	0	0	0	0	0	1	1	0	0	1	1	1	0	1	1	0	1	0	1	0	1	0	1	1	0	3	
<i>P. iriomotense</i>	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1	1	0	?	?	0	1	0	2
<i>P. kabiramm</i>	0	0	2	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	1	3	
<i>P. jakobsenae</i>	0	0	2	1	0	1	1	?	0	0	?	?	?	1	0	0	1	1	1	0	0	1	1	1	0	1	0	0	1	1	0	3	
<i>P. rudmani</i>	1	0	2	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	3	
<i>P. acanthorhinum n. sp.</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1
<i>P. undulatum n. sp.</i>	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	2	?	0	1	0	0	1	0	0	0	0	1	1	1	2	
<i>P. tuberculatum</i>	0	0	2	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	0	1	0	0	1	
<i>P. pinnatum</i>	0	0	2	1	1	1	1	0	2	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	1	0	1	1	
<i>P. karenae</i>	0	0	2	1	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	1	1	0	1	0	0	1	0	1	1	

Lizard Island, Great Barrier Reef, Australia (Wägele et al., 2006).

Etymology

This species was named after the spiny appearance of the papillae on the surface of the rhinophores.

Natural history

Specimens were all found in shallow water on vertical walls with miscellaneous red algae. The wall where specimen 099093 was found was near a bottom covered with a live, stony coral reef, whereas the others were found in a rocky cut near shore. The diet of this species is still unknown.

Description

Color and external morphology: The living animals are elongate, with edges of the foot extending laterally just beyond the mantle. They range in length from 17 to 28 mm for living animals studied. Preserved specimens examined (CASIZ 104702 include three specimens, two of which were dissected and are later referred to as 104702a and 104702b) were 14 mm (CASIZ 104702a), 8 mm (CASIZ 104702b), and 8 mm (CASIZ 099093).

The anterior portion of the foot margin is broad with short, blunt angular foot corners while the posterior end is tapered to a point.

The body of the living animal, including the rhinophores, oral tentacles, and foot is predominantly transparent with opaque white markings on the dorsum. These markings vary and can appear as white specks or as distinct white lines creating a network along the dorsum and head (Figure 1A). The anterior margin of the foot is white in some specimens, extending to the angular foot corners. The viscera and gonad are readily visible through the mantle tissue.

The cerata are elongate and cylindrical, with larger cerata near the medial region of the dorsum. The digestive gland is undulating and undivided within the cerata and is cream or yellow colored near the body leading to red, and then yellow at the apex of each ceras. The cerata are primarily transparent, with slight blue coloration near the tips and have a cnidosac without nematocysts. The ceratal arrangement consists of arches and rows, with arches forming in the anterior ceratal groups (Figure 8A). The precardiac cerata are grouped into one arch on each side of the body containing 6–7 cerata. The genital aperture is located between the arms of the precardiac arch on the right side of the animal. The renal opening is situated in the



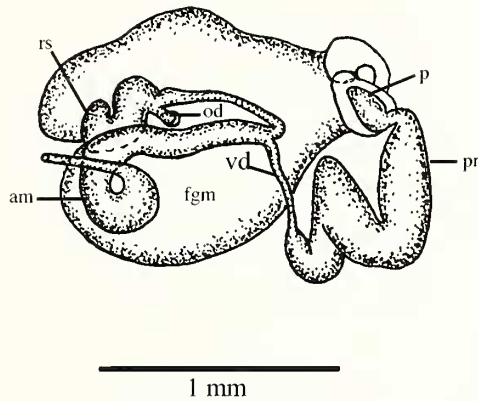
Figure 1. A, *Phyllodesmium acanthorhynchum* n. sp., photo: Robert Bolland; B, *Phyllodesmium undulatum* n. sp., photo: T. Gostmer.

interhepatic space, slightly toward the posterior between the precardiac arch and the first postcardiac arch on the right side. The postcardiac cerata are grouped on both sides into arches containing 5–6 cerata in the first two arches, and 4–5 cerata in the third arch. The anal papilla is located within the first postcardiac arch

on the right side. The fourth postcardiac group appears as a partial arch in some animals and as a row in others containing 3–4 cerata. One or two additional postcardiac ceratal groups appear as rows containing 2–3 cerata.

The rhinophores are conical in shape and are roughly half as long as the oral tentacles. In addition,

A



B

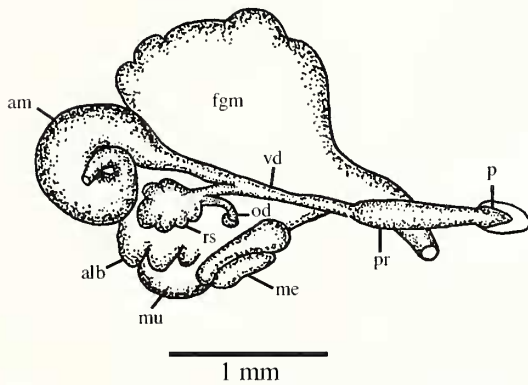


Figure 2. **A**, Reproductive system of *Phyllodesmium acanthorhinum* n. sp.; **B**, Reproductive system of *Phyllodesmium undulatum* n. sp. Abbreviations: *am*, ampulla; *rs*, receptaculum seminis; *od*, oviduct; *vd*, vas deferens; *fgm*, female gland mass; *p*, penial papilla; *pr*, prostate; *alb*, albumen gland; *mu*, mucous gland; *me*, membrane gland.

there are numerous, yellow-cream-colored tubercles on the entire surface of the rhinophores that lead to a yellow-cream, pointed tip. The oral tentacles are smooth, and taper from the anterior edge of the head to pointed apices. They are transparent or slightly bluish basally, leading to white or yellow-cream tips.

Reproductive system (Figure 2A): The large gonad occupies the posterior portion of all specimens. As in most mature animals of this group, the female gland mass is large and consists predominantly of the mucous gland with smaller albumen and membrane glands. The large, looped ampulla branches to the oviduct and the prostatic portion of the vas deferens. The oviduct connects to the S-shaped receptaculum seminis. A second branch extends from near the base of the receptaculum and joins the female gland near the

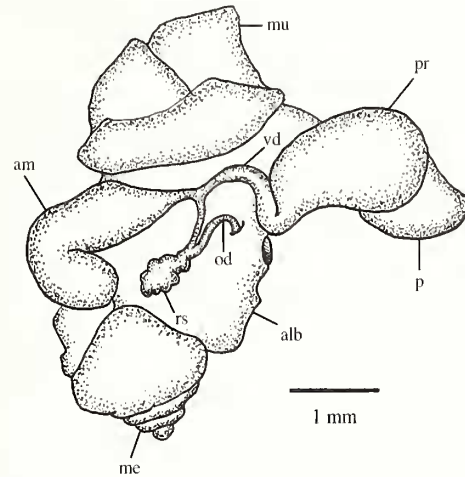


Figure 3. Reproductive system of *Phyllodesmium iriomotense*. Abbreviations: *am*, ampulla; *rs*, receptaculum seminis; *od*, oviduct; *vd*, vas deferens; *p*, penial papilla; *pr*, prostate; *alb*, albumen gland; *mu*, mucous gland; *me*, membrane gland.

albumen gland. The second branch of the ampulla connects to the vas deferens. The proximal portion is prostatic with the prostate being highly convoluted and prominent, with a short, conical-shaped penial bulb.

Buccal armature: The jaws are thin and coriaceous. There are four to seven knobby denticles situated along the masticatory border of each jaw (Figure 4A, B). The radulae have a formula of $33 \times 0.1.0$ for specimen 104702b and $34 \times 0.1.0$ for specimen 099093 (specimen 104702a had a radular formula of $19 \times 0.1.0$; however, this may be an incomplete radula). The teeth are triangular in shape leading to a pointed and slightly curved primary cusp. The rib on the ventral side of each tooth extends from the posterior of the tooth to the apex of the cusp in some specimens and in others stops slightly short of the apex. Denticulation extends along the margin from the base of the tooth nearly to the apex. The number of denticles varies between specimens. Specimen 104702a has 19–28 denticles (Figure 5A). 104702b has 19–22 denticles (Figure 5B), and 099093 has 25–28 denticles per radular tooth. The denticles vary in appearance and can be triangular and broad, with well-separated points or slightly elongated with closely spaced denticles that reach slightly under the edge of the tooth (Figure 5A, B). The denticles at the base of the tooth are generally more defined, where denticles near the apex of the cusp are fused together in some specimens.

Remarks: Of the previously described species of *Phyllodesmium*, there are only two, *Phyllodesmium horridum* (Macnae, 1954), and *Phyllodesmium opalescens* Rudman, 1991, that have undivided digestive tissue within the cerata. Rudman (1981, 1991) described *P.*

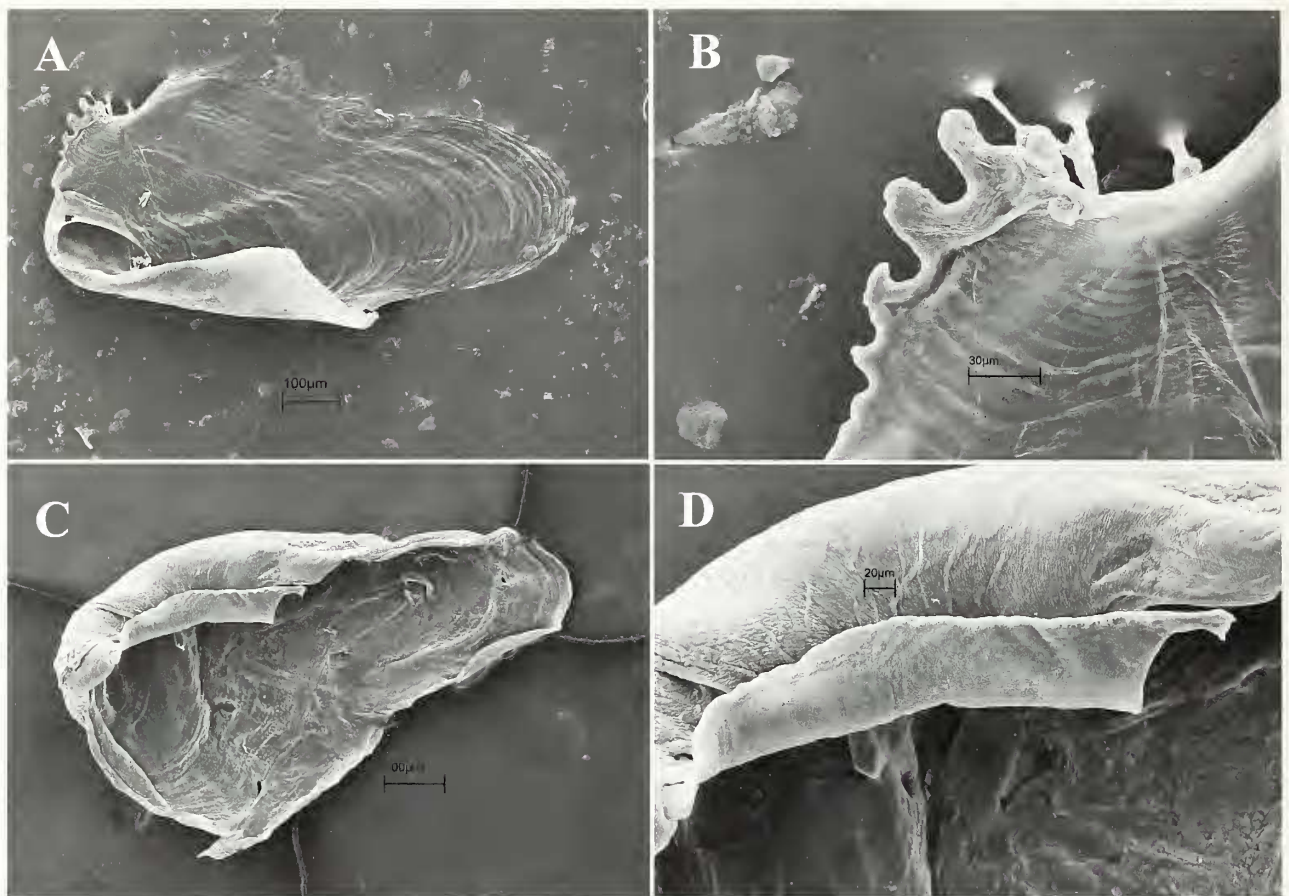


Figure 4. A and B, Jaw plate and masticatory denticles of *Phyllodesmium acanthorhinum* n. sp. (CASIZ 099093); C and D, Jaw plate and masticatory border of *Phyllodesmium undulatum* n. sp. (CASIZ 105746).

horridum as pale translucent, which is notably different from the predominantly transparent mantle of *P. acanthorhinum*. The digestive gland undulates noticeably, without nodulation, in cerata of *P. acanthorhinum*, compared to the straight and sometimes nodulose digestive gland in cerata of *P. horridum*. In addition, *P. horridum* and *P. opalescens* have smooth rhinophores, unlike the rhinophores of *P. acanthorhinum*, which are covered in papillae. The body and cerata of *P. opalescens* are superficially similar to *P. acanthorhinum* in coloration and transparency, but the digestive gland within the cerata of *P. opalescens* is generally straight, with little or no undulation. Also, the opaque white markings along the dorsum of *P. opalescens* are individual diamond- or teardrop-shaped spots running the length of the dorsum. *Phyllodesmium acanthorhinum* has many white flecks, or thin lines creating a network along the dorsum. The reproductive system of *P. acanthorhinum* also differs from the drawings of *P. opalescens* and *P. horridum* shown by Rudman (1981, 1991). The prostate is highly convoluted compared to

that of *P. horridum*, and the receptaculum seminis is notably S-shaped in contrast to the teardrop-shaped structure in *P. opalescens*. Also worth noting in these papers is the incorrect labeling of the receptaculum seminis as a bursa copulatrix. The structure is found a good distance from the genital opening and is connected to the female gland by the oviduct in these animals, indicating it should be described as a receptaculum seminis.

Phyllodesmium undulatum n. sp.

(Figures 1B; 2B; 4C, D; 5C, D; 8B)

Phyllodesmium sp. 4 Gosliner et al, 2008: 389, top three photos.

Material examined

Holotype: California Academy of Sciences, CASIZ 177171, not dissected, 14 m depth, Waterfall Bay,

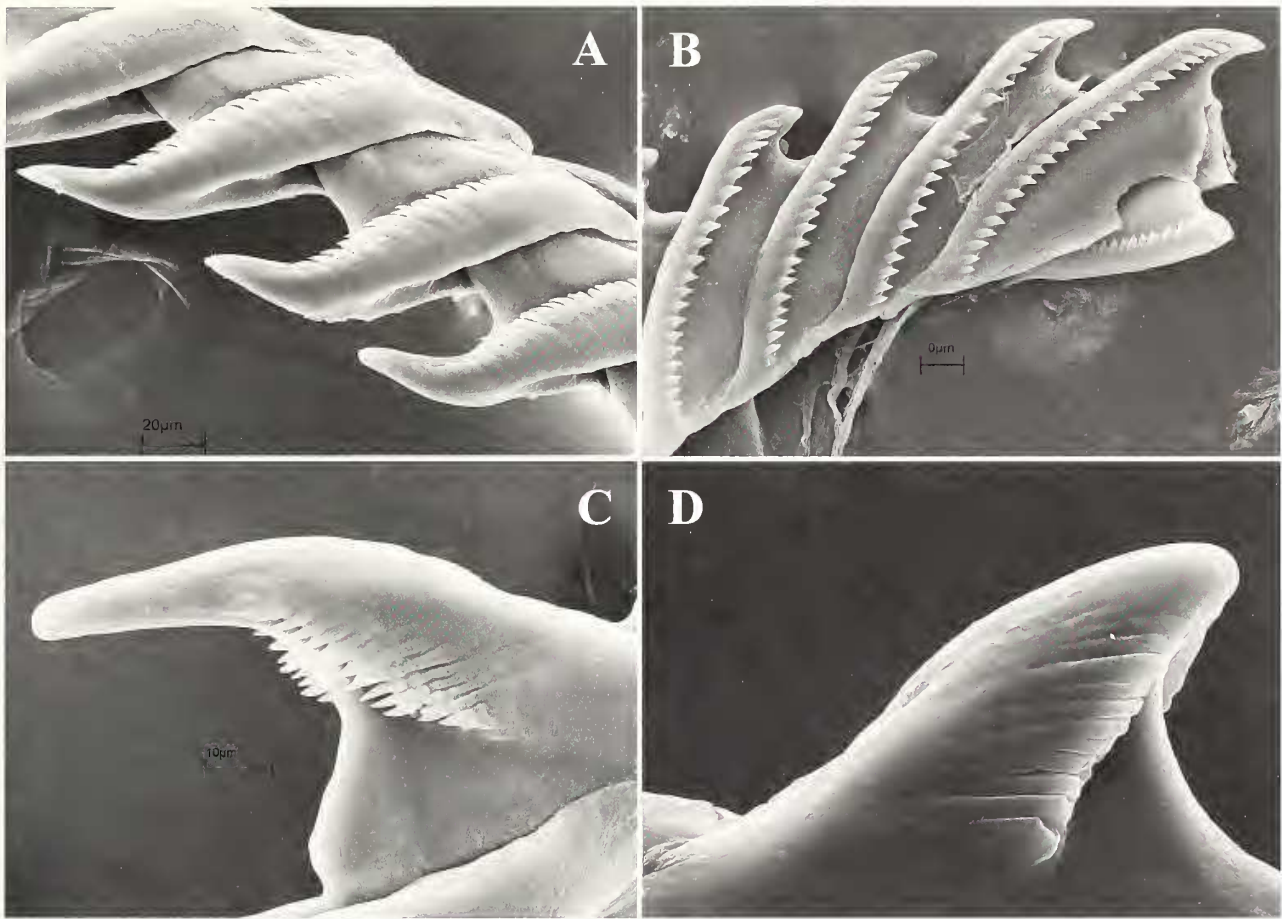


Figure 5. A and B, Radular cusps and denticles of *Phyllodesmium acanthorhinum* n. sp. (CASIZ 104702a and CASIZ 104702b, respectively; note the variation between specimens); C and D, Radular cusps and denticles of *Phyllodesmium undulatum* n. sp. (CASIZ 105746 and CASIZ 115810, respectively; note wear on denticles in image D).

Pulau Tioman, Malaysia, 4 October 2007, T. M. Gosliner.

Paratypes: CASIZ 105746, 0–17 m depth, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 24 February 1995, T.M. Gosliner. CASIZ 115810, 12 m depth, beneath Tengan pier 14 km west of Ikei-shima, Okinawa, Ryukyu Islands, Japan, 25 June 1995, R. F. Bolland. CASIZ 176717, 14 m depth, Waterfall Bay, Pulau Tioman, Malaysia, 4 October 2007, T. M. Gosliner.

Geographic range

Known from Sepok, on Maricaban Island off southern Luzon, Philippines, near Ikei-shima in the Ryukyu Islands, Japan, and Waterfall Bay, Pulau Tioman, Malaysia (present study). There is one photograph of this species from Manado, Indonesia, taken by Pauline Fiene in 1991, but there are no specimens available from this region.

Etymology

This species is named in recognition of the extensively undulating digestive duct within the cerata.

Natural history

Specimens are often found crawling on a red gorgonian octocoral in the genus *Acabaria*. This is likely the prey of this species, but actual feeding has not been observed.

Description

Color and external morphology: Living animals are very elongate with the mantle extending laterally just beyond the narrow foot. Preserved specimens are 15 mm (CASIZ 105746), 18 mm (CASIZ 115810), and 45 mm (CASIZ 176717) in length. The length of specimen 115801 when living was 46 mm. The anterior

portion of the foot margin is broad with moderately tentacular foot corners.

The body of the living animal is predominantly transparent, with viscera and gonads visible through the mantle and foot. A single thin, opaque white line follows the entire length of the animal middorsally between the rhinophores and along the dorsum. The anterior foot corners have a cream-yellow line extending from the lateral sides of the head to the tips of the tentacular processes (Figure 1B).

The cerata are generally transparent with the exception of a slight blue color near the tips followed by yellow at the terminus of each ceras. They are cylindrical and contain extensively undulating and undivided digestive tissue. The digestive gland within each ceras is a cream-yellow color near the dorsum, turns slightly pink just before the blue portion of the ceras, and turns cream-yellow again at the tip of the ceras. The cerata contain distinctive but nonfunctional endosacs at the distal ends. The longest and widest cerata are near the median region of the dorsum, with newly developing cerata at the edge of the mantle. The ceratal arrangement consists of arches and rows, with anteriormost groups forming arches and posteriormost groups forming rows (Figure 8B). One specimen (CASIZ 115810) was missing all cerata, but the raised basal groupings appear consistent with the other specimens. The precardiac and first postcardiac arches both contain 7–11 cerata, with the largest animal (CASIZ 176717) having ceratal groups containing the most cerata, and the smallest animal (CASIZ 105746) with the least. The genital aperture is located just anterior to the precardiac arch on the right side. The renal pore is in the interhepatic space between the precardiac and first postcardiac arches on the right side, slightly closer to the postcardiac group of cerata. The anal papilla is directly under the first postcardiac arch on the right side. The second postcardiac ceratal arch contains 6–11 cerata, followed by 5–10 cerata in the third postcardiac arch. The fourth postcardiac ceratal group contains 5–7 cerata and is an incomplete arch, while the fifth and sixth postcardiac groups each contain 2–3 cerata in rows (specimen number 105746 had only one ceras in the fourth, fifth, and sixth postcardiac ceratal groups, but this was suspected to be due to prior injury). Specimen number 176717, being the largest specimen, had a seventh postcardiac ceratal row containing three cerata. The oral tentacles and rhinophores are smooth, and taper to pointed apices. The rhinophores are extended in length, as long as the oral tentacles in preserved specimens, and both are generally transparent with variable blue and/or yellow bands. Two specimens (CASIZ 105746 and 176717) have only yellow on the rhinophores, whereas the other has a hint of blue midway up each rhinophore. The oral tentacles and rhinophores terminate in broadly yellow tips for all specimens.

Reproductive system (Figure 2B): All three dissected specimens were mature, with well-developed female glands consisting mostly of mucous gland. The albumen and membrane glands were completely developed but smaller in comparison. A large, looped ampulla branches to the oviduct and the prostatic portion of the vas deferens. The oviduct joins a nodulose receptaculum seminis, and a second branch extends from the base of the receptaculum to join the mucous gland near the albumen gland. The second branch of the ampulla connects to the vas deferens with the proximal portion being prostatic. The moderately sized prostate is slightly convoluted in two specimens (CASIZ 115810 and 176717) and totally straight in the other (CASIZ 105746), leading to a small, conical-shaped penial bulb in both specimens. The genital aperture has two openings, one each for the male and female genital systems (Figure 2B).

Buccal armature: The jaws are thin and coriaceous with undeveloped, possibly vestigial, bumps on the masticatory border. These are not denticulate, but noticeable in both specimens (Figure 4C, D). The radulae have formulae $17 \times 0.1.0$ for specimen 105746 and $22 \times 0.1.0$ for specimen 115810. The radular teeth are triangular in shape leading to long, slightly curved, primary cusps in one specimen (105746; Figure 5C) and blunt, short primary cusps in the other (115810; Figure 5D). The latter specimen appears to have an abnormality in the length of the primary cusp, or this may have been caused by severe wear on the teeth. The rib on the ventral side of each tooth extends from the posterior of the tooth to the point of curvature on the primary cusp in specimen 105746. In the specimen with the blunt, short primary cusp, the ventral rib extends nearly to the apex. Denticulation extends along the margin of each tooth, starting at the base of the tooth and ending at the curvature of the primary cusp in one specimen, and nearly to the apex of the cusp in the other. The denticles numbered 12–14 in specimen 105746 and 10–14 in specimen 115810. The denticles are elongate and pointed, reaching slightly underneath the ventral portion of the tooth in specimen 105746, and appear shorter and more blunt in specimen 115810. This further indicates increased wear on the teeth in the latter specimen.

Remarks: Of the previously described species of *Phyllodesmium*, only *P. opalescens*, *P. horridum*, and *P. acanthorhinum* have undivided digestive tissue within the cerata. However, in 1991, Rudman noted the presence of nodules or buds on the digestive gland in *P. horridum*, which are not seen in *P. opalescens* or in the new species, *P. undulatum* and *P. acanthorhinum*. In addition, the predominantly transparent mantle and cerata of *P. undulatum* varies noticeably from the translucent and pale appearance of the mantle in *P.*

horridum. When compared to *P. opalesceus*, *P. undulatum* differs noticeably in a number of ways. Externally, the digestive tissue within the cerata of *P. undulatum* undulates unmistakably whereas in *P. opalesceus* the tissue is relatively straight. Also, the opaque white line down the dorsum of *P. undulatum* is different from the distinctive white diamonds or teardrop-shaped patches down the dorsum of *P. opalesceus*. The jaw structure of *P. opalesceus* includes large, blunt denticles (Rudman, 1991), whereas the jaw of *P. undulatum* has no obvious denticles. The reproductive system of *P. opalesceus* and *P. undulatum* also differ, as *P. undulatum* has a nodulose receptaculum seminis and a moderate, predominantly straight prostate. *Phyllodesmium opalesceus* has a smooth receptaculum seminis and a prominent, highly convoluted prostate. When externally comparing *P. undulatum* and *P. acauthorhiuum*, they can be easily distinguished by the papillate rhinophores in *P. acauthorhiuum* compared with the smooth rhinophores in *P. undulatum*, and by the single white line down the dorsum of *P. undulatum* and the network or flecked pattern on the dorsum of *P. acauthorhiuum*. Additionally, *P. undulatum* has elongate angular foot corners, whereas those of *P. acauthorhiuum* are short and blunt. Their reproductive systems also vary. *Phyllodesmium undulatum* has a nodulose receptaculum seminis and a straight, moderately sized prostate, whereas *P. acauthorhiuum* has an S-shaped receptaculum seminis and prominent, convoluted prostate. The jaw morphology is definitive based on the absence of masticatory denticles in *P. undulatum* and 4–7 knobby denticles in *P. acauthorhiuum*.

Phyllodesmium iriomotense Baba, 1991

(Figure 3)

Material examined

One specimen, CASIZ 84878, 59 m depth, Seragaki Beach 1.3 km ENE of Maeki-zaki, Okinawa, Japan, 16 October 1991, R. F. Bolland.

Geographic range

This species is known only from its type locality Okinawa, Japan (Baba, 1991b).

Further description

Although Baba created very detailed drawings of *P. iriomotense*, he did not include any data about the reproductive system of this species (Baba, 1991b: figs. 6,7).

Description

Reproductive system (Figure 3): The specimen was mature, with well-developed female glands consisting mostly of mucous gland. The albumen and membrane glands were completely developed but smaller in comparison. A large, hook-shaped ampulla branches to the oviduct and the prostatic portion of the vas deferens. The oviduct joins a small, nodulose receptaculum seminis, and a second duct extends from the base of the receptaculum to join the albumen gland. The second branch of the ampulla connects to the vas deferens with the proximal portion being prostatic. The prostate is large and slightly convoluted in the distal-most portion, leading to a large, conical-shaped penial bulb. The genital aperture has only one opening for the male and female genital systems.

PHYLOGENETIC ANALYSIS

In the present study, 23 species of *Phyllodesmium* are examined. This includes *P. acauthorhiuum* and *P. undulatum*. The two new additions were included in the final matrix to produce an updated phylogeny (Figure 6).

Characters and their states were as follows:

1. Body size: Refers to the overall length of the animal. A distinct gap appears to be evident between species that are smaller than 40 mm and those that are usually 50–100 mm in length.
0 = Less than 40 mm
1 = 40 mm or greater
2. Foot width: Refers to the width of the foot in relation to the mantle and body.
0 = wider than mantle
1 = the same width as, or narrower than the mantle
3. Digestive gland: Refers to the degree of ramification in the duct of the cerata. The unbranched state is suspected to be the plesiomorphic state (Rudman, 1991).
0 = unbranched
1 = branched
2 = secondarily branched or further ramified
4. Zooxanthellae: Refers to the presence or absence of zooxanthellae in digestive diverticula. The absence of zooxanthellae is suspected to be the plesiomorphic state (Rudman, 1991).
0 = absent
1 = present
5. Ceratal texture: Refers to the texture of the external ceratal surface.
0 = smooth
1 = nodulose, with distinct tubercles or papillae
6. Ceratal shape: Refers to the shape of an individual ceras.

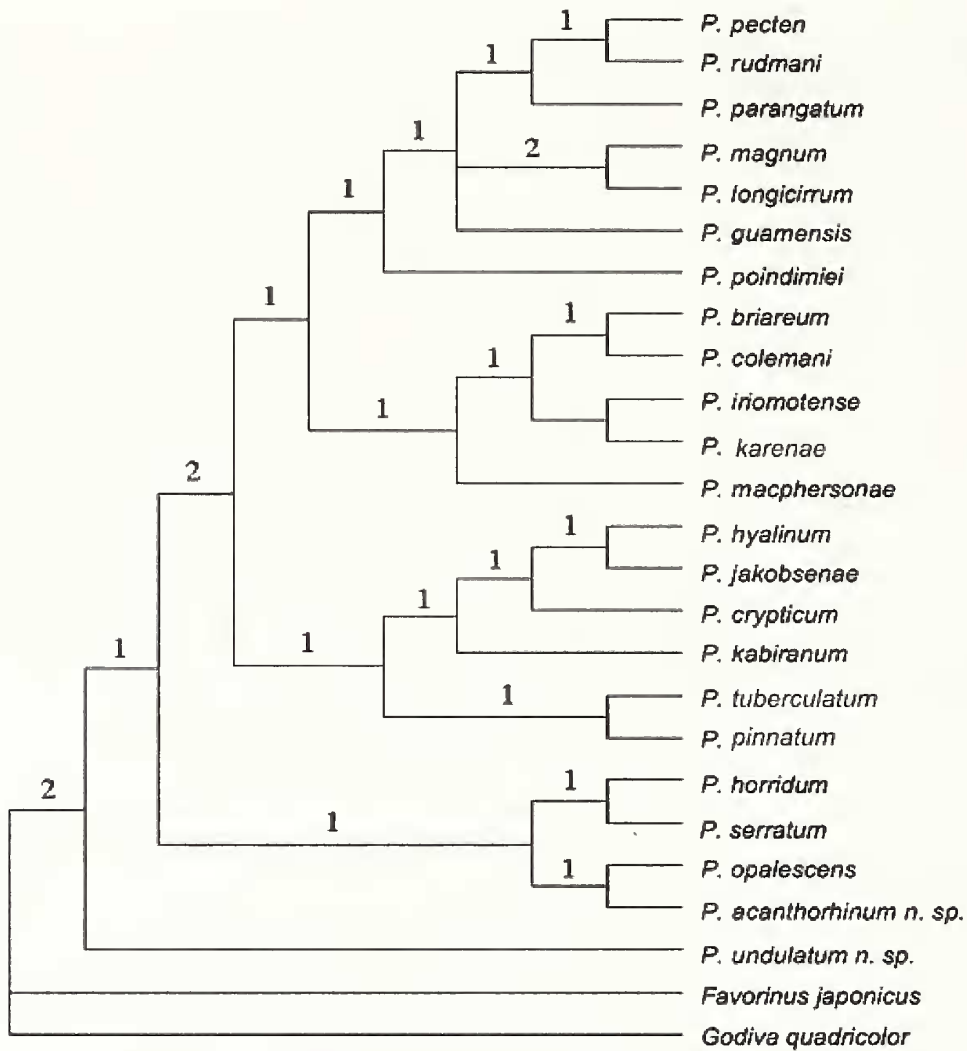


Figure 6. Strict consensus of two most parsimonious trees. L = 111, CI = 0.306, RI = 0.601. Numbers above branches are decay analysis values.

- 0 = cylindrical
- 1 = flattened
- 7. Ceratal apex: Refers to the shape of the tips of the cerata. Based on comparisons of many photos of living animals in varied states of activity. Species listed as having curved or curled ceratal apices consistently exhibit this arrangement.
 - 0 = straight
 - 1 = curved or curled
- 8. Cnidosac: Refers to the presence or absence of a functional cnidosac. Presence of a functional cnidosac is suspected to be the plesiomorphic state (Rudman, 1991).
 - 0 = present and nonfunctional
 - 1 = present and functional
- 9. Shape of digestive gland duct: Refers to the presence or absence of undulation in the digestive diverticula of the cerata.
 - 0 = straight
 - 1 = undulating
- 10. Precardiac cerata: Refers to the shape of the anteriormost ceratal grouping. Arch-shaped ceratal groups are suspected to be the plesiomorphic state (Rudman, 1991).
 - 0 = arch-shaped
 - 1 = not arch-shaped
- 11. Postcardiac cerata: Refers to the shape of the first postcardiac ceratal grouping. Arch-shaped ceratal groups are suspected to be the plesiomorphic state (Rudman, 1991).
 - 0 = arch-shaped
 - 1 = not arch-shaped
- 12. Second group of cerata: Refers to the shape of the second postcardiac ceratal grouping. Arch-shaped

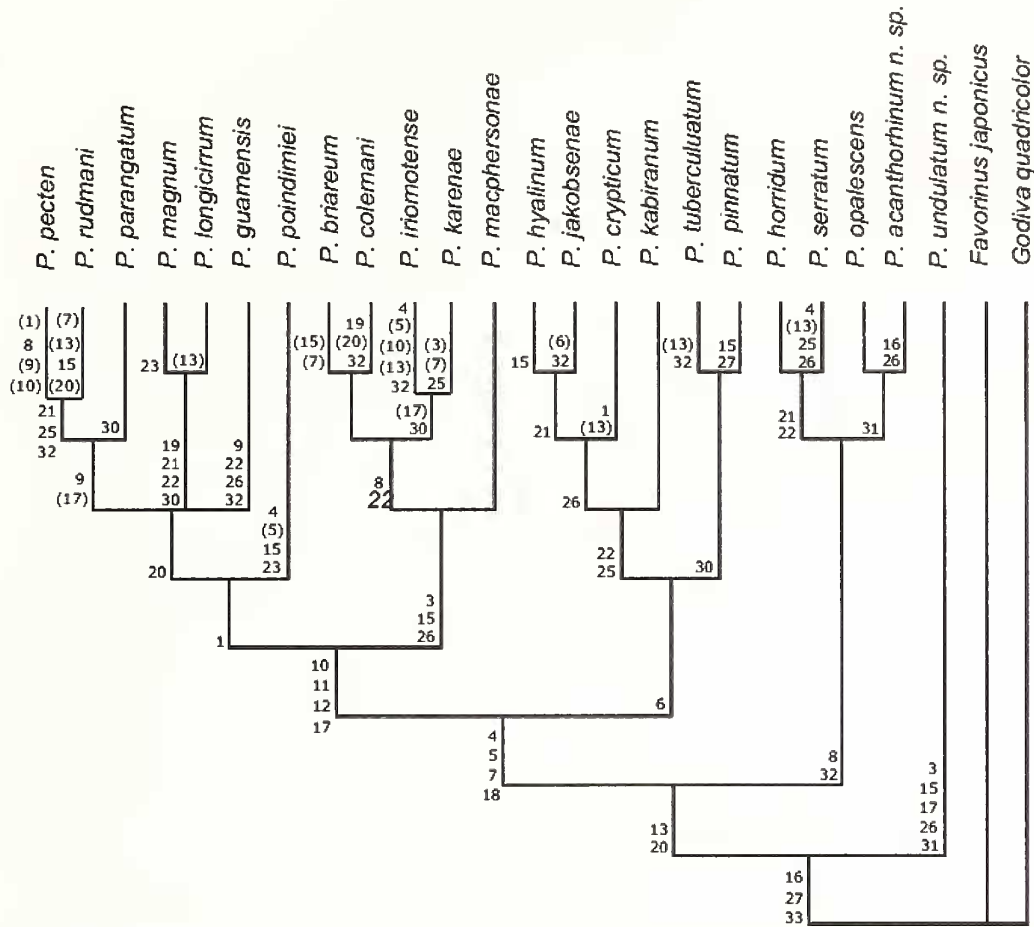


Figure 7. Consensus tree with map of characters. Numbers correspond to character numbers listed in the phylogenetic analysis. Numbers in parentheses are reversals. In cases where changes followed an equivocal node, the changes were treated as regular changes, not reversals.

ceratal groups are suspected to be the plesiomorphic state (Rudman, 1991).

- 0 = arch-shaped
- 1 = not arch-shaped

13. Third group of cerata: Refers to the shape of the third postcardiac ceratal grouping. Arch-shaped ceratal groups are suspected to be the plesiomorphic state (Rudman, 1991).

- 0 = arch-shaped
- 1 = not arch-shaped

14. Anterior foot corners: Refers to the shape of the anterior foot corners.

- 0 = moderately tentacular or tentacular
- 1 = not tentacular

15. Anus position: Refers to the location of the anus. (This character was uninformative as it is autapomorphic for *P. hyalinum*.)

- 0 = within ceratal grouping
- 1 = dorsal to ceratal grouping

16. Rhinophore size: Refers to the length of the rhinophores. Species that have rhinophores that are as long as or longer than the oral tentacles are considered to be greatly extended.

- 0 = moderately long
- 1 = greatly extended

17. Rhinophore surface: Refers to the texture on the surface of the rhinophores.

- 0 = ornamented
- 1 = smooth

18. Masticatory border: Refers to the number of rows of denticles on the jaw plate.

- 0 = many rows of denticles
- 1 = one row of denticles
- 2 = smooth (no rows)

19. Jaw denticles: Refers to the overall appearance of the jaw denticles.

- 0 = uniform size, or evenly graded
- 1 = obvious size gradient

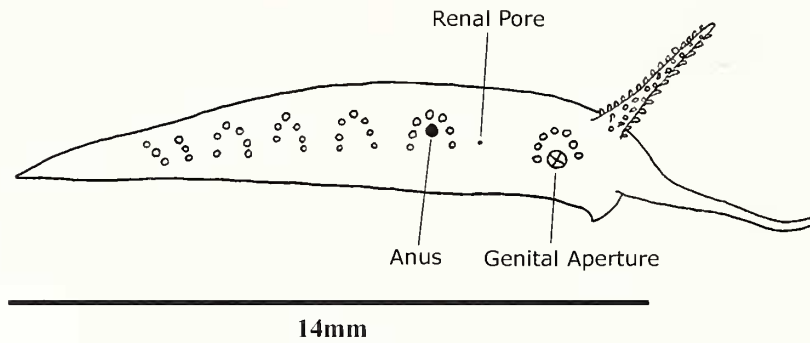
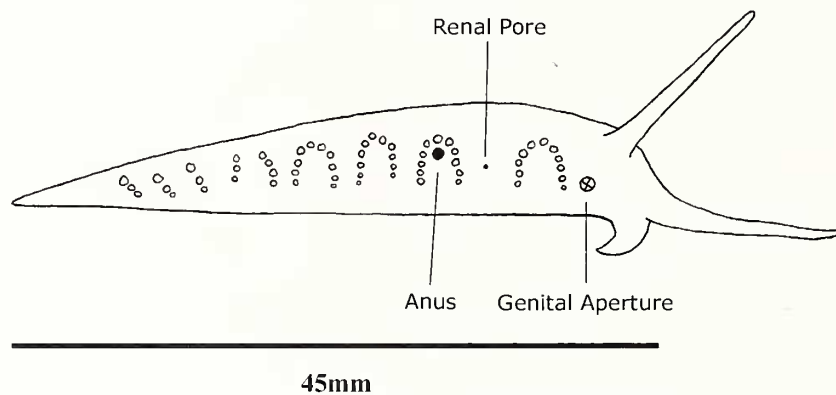
A**B**

Figure 8. Lateral view of preserved specimens showing ceratal arrangement. **A**, *Phylloidesmium acanthorhimum* n. sp. (CASIZ 104702a); **B**, *Phylloidesmium unclatum* n. sp. (CASIZ 176717). Scale bars represent preserved specimen length.

- | | |
|---|--|
| <p>20. Radular denticles: Refers to the overall appearance of the radular denticles.
0 = well developed
1 = reduced or absent</p> <p>21. Cusp of teeth: Refers to the location of denticles on the radular cusp.
0 = denticulate nearly to apex
1 = denticulate only well below apex</p> <p>22. Arrangement of radular denticles: Refers to the spacing between radular denticles.
0 = well separated
1 = congested</p> | <p>23. Length of radular denticles: Refers to the length of the radular denticles.
0 = elongate, longer than wide
1 = short, width equal to or wider than length</p> <p>24. Tip of radular denticles: Refers to the shape of the tips of the radular denticles.
0 = blunt
1 = pointed</p> <p>25. Rows of radular denticles: Refers to the number of rows of radular denticles. (This character was uninformative as it is autapomorphic for <i>Phylloidesmium guamensis</i> Avila et al., 1998.)</p> |
|---|--|

- 0 = one
1 = two
26. Base shape of teeth: Refers to the shape of the base of the radular cusps.
0 = triangular
1 = horseshoe-shaped
27. Base limb length of teeth: Refers to the length of the base of the radular cusps.
0 = longer than cuspidate portion bearing denticles
1 = shorter than cuspidate portion bearing denticles
28. Penial spine: Refers to the presence or absence of a penial spine. (This character was uninformative as it is autapomorphic for *Godiva quadricolor*.)
0 = absent
1 = present
29. Female gland shape: Refers to the overall shape of the female gland mass (This character was uninformative as it is autapomorphic for *Phylloidesmium macphersonae* Burn, 1962.)
0 = elongate
1 = bulbous
30. Penial papilla: Refers to the size of the penial papilla.
0 = large, much wider than the vas deferens
1 = small, equal in width to vas deferens or narrower
31. Prostate length: Refers to the length of the prostate.
0 = long, generally consisting of two or more deep convolutions
1 = short, with one or no shallow convolutions
32. Prey: Refers to the kind of prey consumed.
0 = other
1 = octocorals generally
2 = only gorgonians
3 = only soft corals
4 = only stoloniferans

Parsimony analysis revealed two most parsimonious trees with 111 steps. The permutation tail probability test revealed a $P = 0.01$ chance that the tree could be reproduced with random data. The character trace tree is shown in Figure 7. The consistency index was 0.306 and the retention index was 0.601. Decay analysis results are shown in Figure 6.

DISCUSSION

Based on the phylogeny presented in this study, the genus *Phylloidesmium* is a monophyletic group (Figure 6) with *P. undulatum* as the most basal species in the phylogeny. This is expected due to the undivided digestive duct within cerata of this species, and the lack of zooxanthellae found within nudibranch tissues. *Phylloidesmium acanthorhinum* is in a clade along with

P. opalescens, *P. horridum*, and *Phylloidesmium serratum* (Baba, 1949), which are all basal in comparison to species with branched digestive tissue and symbiosis with zooxanthellae. The permutation tail probability test indicates that the dataset is significantly different from randomness, and is thus informative.

Generally, this phylogeny is in accordance with the strict consensus tree produced by Ortiz & Gosliner (2008) with the exception of a few differences. In the present tree, the relationship between *Phylloidesmium parangatum* Ortiz & Gosliner, 2003, *Phylloidesmium jakobsenae* Burghardt & Wägele, 2004, and *Phylloidesmium rudmani* Burghardt & Gosliner, 2006 is fully resolved. However, the placement of these species is different, with *P. jakobsenae* clustering within a clade of species that mimic *Xenia* corals, and *P. rudmani* clustering with *Phylloidesmium pecten* Rudman, 1981 and *P. parangatum*. In addition, the relationship between *Phylloidesmium poindimiei* (Risbec, 1928), *P. briareum*, and *P. macphersonae* is also fully resolved in a clade that also includes *P. sp. 3*. As was seen in Ortiz & Gosliner (2008), *Phylloidesmium* appears to be monophyletic with a decay value of 2, supported by characters 16, 27, and 33 (Figure 7).

As was suggested by Rudman (1991), species with the highest degree of digestive gland ramification and dense populations of zooxanthellae appear to be the most highly derived. This is supported by characters 4, 5, 7, and 18 at the node dividing the nonsymbiotic species from symbiotic, and also has a higher decay value than most of the surrounding nodes. *Phylloidesmium longicirrum* and *Phylloidesmium magnum* Rudmani, 1991 also form a moderately supported clade within a trichotomy that includes the most highly derived species. This is not surprising due to the flattened cerata and highly ramified digestive diverticula present in these species. These attributes allow the animals to provide maximum sunlight to large populations of symbiotic zooxanthellae, likely maximizing their photosynthetic output. The large body size of *P. longicirrum* and *P. magnum* may also suggest that the additional nutrients provided by the symbionts allow the animal to achieve greater size, further indicating a highly advanced relationship with the alga. In addition, *P. hyalinum*, *P. jakobsenae*, *Phylloidesmium crypticum* Rudman, 1981, and *Phylloidesmium kabiramm* Baba, 1991, which all have cerata that mimic *Xenia* or *Heteroxenia* coral polyps, are grouped into an exclusive, but moderately derived clade. *Phylloidesmium crypticum* and *P. hyalinum* are considered moderately advanced in their symbiont retention abilities (Kempf, 1991), which is in accordance with their placement in this phylogeny. However, Burghardt & Wägele (2004) suggest that *P. jakobsenae* is further advanced in its symbiosis with zooxanthellae than *P. crypticum* or *P. hyalinum*, indicating it may be more derived than

presently shown. *Phyllodesmium poindimiei* and *P. iriomotense*, which do not harbor zooxanthellae but have moderately ramified digestive tissue, appear in clades with species that have moderate to advanced symbioses with zooxanthellae. The inclusion of *P. poindimiei* in such a derived clade is not well supported, and is only upheld by character 1. However, the resolution for that entire clade is generally low (Figures 6 and 7), indicating it could easily be altered with the addition of new taxa or characters. Despite the lack of support, the placement of *P. poindimiei* and *P. iriomotense* is interesting, suggesting a possible reversal from a symbiotic to nonsymbiotic state. This reversal is especially evident on the character trace tree at *P. iriomotense*, as there are five character state changes seen in this species, three of which are reversals (Figure 7).

Despite the general trend showing the advancement of species with symbioses and the clustering of *Xenia*-mimicking species, the obvious trichotomy and the low decay analysis values indicate that some resolution and robustness is still lacking. Although the results of the permutation tail probability test indicate the tree is informative, the consistency and retention indices are both low, further indicating that the fit of the characters to this tree is not highly robust. *Phyllodesmium rudmani*, which has arguably the most cryptic cerata among all of the *Xenia* mimics, clusters with *P. pecten* and *P. parangatum* in a more derived portion of the tree.

Although the outgroup for this analysis was chosen based on a suspected close relationship with *Phyllodesmium* and prior usage by Ortiz & Gosliner (2008), the sister group to *Phyllodesmium* has not yet been determined and other outgroups may yield varied results. This problem was especially apparent when mapping the characters on the tree, as many character reversals could not be fully identified due to differing character states within the two outgroup species. In addition, character number 33 was deleted from the character trace tree as the state is unknown in some species and it varies greatly within the ingroup.

Regardless of the diversity in the genus *Phyllodesmium*, there are highly conserved morphological features among the species, and accurately identifying subtle differences is a serious challenge. Molecular investigation would likely shed some light onto the evolutionary history of this group and allow further distinctions between lineages. In addition, many species of *Phyllodesmium* remain to be described, leaving important information missing from a comprehensive phylogeny.

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